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Effects of *Lantana camara* invasion on vegetation diversity and composition in the Vhembe Biosphere Reserve, Limpopo Province of South Africa

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ABSTRACT

Although the effects of invasive alien plants on natural ecosystems are widely acknowledged, the effects of specific plant species can be context dependent. The study examined changes in native vegetation diversity and composition following *Lantana camara* invasion at different cover conditions in the Vhembe Biosphere Reserve, Limpopo Province of South Africa. Using a comparative approach, native vegetation diversity, cover, and composition were compared in *L. camara* high and low cover and uninvaded conditions, on three replicated sites, each with five 10 × 10 m plots. Results show that vegetation diversity (species richness, Shannon-Wiener, and evenness index) were significantly higher in the uninvaded condition than in the *L. camara* high and low invasion conditions. Species relative cover was significantly higher in uninvaded condition than in *L. camara* high and low invasion conditions, though it decreased gradually along the invasion cover gradient for trees and shrubs as well as forbs. Analysis of similarities showed significant separations in vegetation composition among the three invasion conditions for all the growth forms, with most woody alien plants, e.g. *Acacia mearnsii, Rubus rigidus*, and *Caesalpinia decapetala* being associated with *L. camara* high and low invasion conditions. The study concludes that invasion by *L. camara* was associated with changes in native vegetation diversity, cover, and composition, with observed changes being more visible under *L. camara* high as compared to low invasion condition. The presence of *L. camara* at high cover condition significantly decreased native species diversity and composition, an indication that impacts of *L. camara* invasion are cover dependent. From a management standpoint, the study suggests the removal of *L. camara*, however such removal should consider protecting the co-occurring native species. This study offers a baseline for further research to determine mechanisms responsible for native vegetation change associated with *L. camara* invasion.

Introduction

Invasive alien species are posing a threat to natural ecosystems, which are already threatened by habitat and land use change due to human population increase [1,2]. To date, invasive alien species are regarded as one of the top five causes

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of biodiversity loss [2,3]. Recent reports have shown that invasive alien plants have caused tremendous socio-economic and environmental consequences globally [4]. Although the impacts of invasive alien plants, on natural ecosystems are site and species specific, the general observation is that many invasive alien plants trigger changes in ecosystem structure, functioning, and composition [5,6], resulting in a significant decline in native species diversity [7]. In some cases, invasive alien plants transform the ecosystem resulting in modified ecosystems that produce limited ecosystem services [8,9]. At ecosystem level, impacts of invasive plant species include changes to soil properties [10,11], hydrology [12], and fire regimes [13]. At community level, invasive plant species have been shown to reduce native species diversity and composition [14], though such impacts can be species or site specific. On the contrary, facilitation and co-occurrence between invasive (at low invasion densities and cover) and native plants has been reported [15], this as a result of positive interactions among plant species with similar habitat requirements and phenologies. For example, Leger [16] reported that the invasive grass *Bromus tectorum* can co-occur with the native grass *Elymus multisetus*. Similarly, Sholto-Douglas et al. [17] observed that the invasive shrub *Aspalathus subtingens* act as a nurse and refuge plant for native plants, thus facilitating species co-occurrence. The above-mentioned mixed responses show that invasive plant species can cause positive or negative impacts on ecosystems. Therefore, this calls for further investigations to examine the nature of invasive alien plant impacts, in order to develop effective control strategies.

In South Africa, *Lantana camara* L. (sensu lato) (Verbenaceae) has been identified as a problematic invasive shrub, but our understanding of the plant and its invasion impacts on natural ecosystems is limited and biased in favour of a few biomes, notably in the savanna and grassland [18]. Few studies have been conducted to examine community level effects of *L. camara* invasion on South African ecosystems [19,20], yet the species has invaded over 2 million hectares of land and is present in seven of the nine terrestrial biomes of the country [18]. Ruwanza [21] examined the impacts of *L. camara* invasion on native plant species diversity using soil seed bank and results showed that the species reduces native species soil seed bank composition and diversity. Also, Jevon and Shackleton [22] reported that *L. camara* invasion supresses species richness of recruiting native forest species in the Eastern Cape Province of South Africa. To my knowledge, no study in South Africa has examined how increases in *L. camara* cover affect native plant community and diversity, yet previous studies in other countries have shown that the effects of *L. camara* invasion on native ecosystems can be both density and cover dependent [23]. For example, a study in Zimbabwe reported that sites heavily invaded by *L. camara* had significantly lower native species composition and diversity as compared to sites with low *L. camara* invasion [24]. Similarly, Sundaram & Hiremath [25] reported that the fourfold increase in *L. camara* density from 1997 to 2008 in India's Biligiri Rangaswamy Temple wildlife sanctuary resulted in the decline in native species richness, diversity and evenness, thus an indication that increase in invasion density over a 10 year period resulted in a decrease in native species diversity. Changes in native plant species diversity due to increased invasive alien plant density and cover are mostly linked to competition for resources and space caused by alien plants recruitment advantages [26]. Therefore, it is necessary to examine the response of native plant communities to increased *L. camara* cover.

Lantana camara was introduced in South Africa around 1858 in Cape Town, Western Cape Province [27]. The species which originates from tropical and subtropical South and Central America [27,28] has extensively spread in most parts of South Africa [18]. In South Africa, *L. camara* tolerates a wide variety of environmental conditions, though it dominates humid areas with dense population in KwaZulu-Natal, Mpumalanga, Limpopo, and Eastern Cape Provinces of the country [18]. The few studies that have examined the effect of *L. camara* invasion in South Africa have reported that *L. camara* invasion is associated with increases in some soil physico-chemical properties, e.g. total C, total P, moisture, and repellency [20]. Samways et al. [29] noted that *L. camara* invasion decreases invertebrate diversity, while van Wilgen [30] reported an estimated 80% reduction in grazing potential under high *L. camara* invasion in South Africa. A recent study by Ruwanza and Shackleton [31] reported that *L. camara* leaf, stem, and roots release allelopathic compounds that reduce native species germination and establishment.

Comparative studies of invaded and uninvaded areas have been shown to identify potential impacts of invasion on natural ecosystems, thus providing crucial information that can be used to manage invasive alien plants [6,32]. This comparative study aimed to determine changes in native vegetation diversity, cover, and composition following *L. camara* invasion at different cover conditions in the Vhembe Biosphere Reserve, Limpopo Province of South Africa. Specifically changes in native vegetation diversity, cover, and species composition were compared between invaded (high and low cover) and uninvaded conditions. Results of this study are envisaged to inform ecologists, land managers, and policymakers about the effects of *L. camara* invasion on vegetation community in South Africa.

Materials and methods

Study area

The study was conducted on three sites located along the regional road R578 between the towns of Louis Trichardt and Elim in the Limpopo Province, South Africa (Table 1 and Fig. 1). The three sites were selected because they have different *L. camara* invasion cover conditions that are next to each other and were adjacent to uninvaded conditions dominated by indigenous woody native plants. The three sites had similar slope angle (approximately 8°) and soil type (clay) and were at least 10 km apart from each other to allow independence of sampling stations. The sites were at least 25 m away from the

Table 1
Characteristics of the study sites located between Louis Trichardt and Elim in Limpopo Province of South Africa. *Lantana camara* invaded (high and low cover conditions) and uninvaded sites were adjacent to each other.

Site number	Invasion condition	Site name	Coordinates	Site description
Site 1	*L. camara* high invasion	S1-HI	−23.088648, 29.932195	- Site located 7 km from Louis Trichardt along R578 to Elim - High invasion by *L. camara*
Site 1	*L. camara* low invasion	S1-LI	−23.086754, 29.927931	- Site located 7 km from Louis Trichardt along R578 to Elim - Low invasion by *L. camara*
Site 1	Uninvaded	S1-UI	−23.088162, 29.935089	- Site located 7 km from Louis Trichardt along R578 to Elim - Dominated by natural vegetation
Site 2	*L. camara* high invasion	S2-HI	−23.105202, 29.964282	- Site located 12 km from Louis Trichardt along R578 to Elim - High invasion by *L. camara*
Site 2	*L. camara* low invasion	S2-LI	−23.103637, 29.959769	- Site located 12 km from Louis Trichardt along R578 to Elim - Low invasion by *L. camara*
Site 2	Uninvaded	S2-UI	−23.103376, 29.964871	- Site located 12 km from Louis Trichardt along R578 to Elim - dominated by natural vegetation
Site 3	*L. camara* high invasion	S3-HI	−23.114385, 30.009817	- Site located 17 km from Louis Trichardt along R578 to Elim - High invasion by *L. camara*
Site 3	*L. camara* low invasion	S3-LI	−23.112585, 30.006247	- Site located 17 km from Louis Trichardt along R578 to Elim - Low invasion by *L. camara*
Site 3	Uninvaded	S3-UI	−23.111170, 30.001209	- Site located 17 km from Louis Trichardt along R578 to Elim - Dominated by natural vegetation

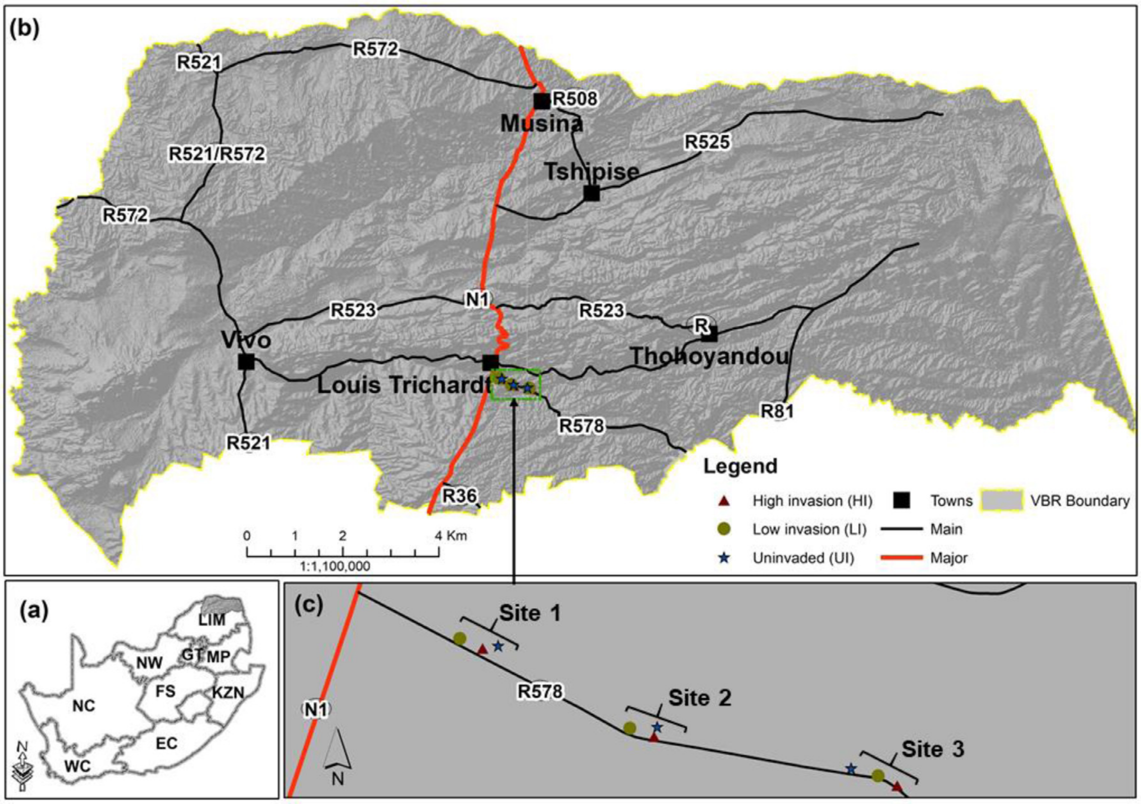

Fig. 1. Map of study area showing (a) South African Provinces, (b) Vhembe Biosphere Reserve, and (c) distribution of study sites (HI – high invasion, LI – low invasion and UNI – uninvaded) along regional road R578.

Table 2
Measurements of aerial visual cover estimates, basal stem diameter, and plant height used to categorize invasion condition. Data for basal stem diameter and plant height are mean ± se.

	High *L. camara* invasion	Low *L. camara* invasion	Uninvaded
Aerial visual cover estimates as a%	>70	<60	>65
Basal stem diameter in cm	7.53 ± 0.12	5.28 ± 0.11	8.20 ± 0.16
Plant height in m	1.53 ± 0.03	0.73 ± 0.07	1.75 ± 0.08

road, this was meant to avoid the role of roadside disturbance, which has been reported to facilitate alien plant invasion [33,34].

The mean annual rainfall in the area is about 1100 mm, with approximately 60% received in summer between October and April [35]. Temperatures are hot in summer (ranging between 16 °C to 40 °C) and mild in winter (ranging between 12 °C to 22 °C). The soils are generally well-drained, acidic, high in clay content, and of Soutpansberg formation. The vegetation in the areas is Soutpansberg Mountain Bushveld, which is found in the savanna biome [35]. The Soutpansberg Mountain Bushveld is dominated by a dense tree layer and poor grass layer [35]. Commonly occurring native species are *Vachellia karroo, Searsia pentheri, Euclea natalensis, Themeda triandra*, and *Cynadon dactylon* [35].

Study design

At each of the three above-mentioned sites, three patches with different vegetation conditions were selected, namely *L. camara* high and low invasion conditions as well as uninvaded condition which acted as the reference site (the three patches are hereafter referred to as (i) *L. camara* high invasion condition, (ii) *L. camara* low invasion condition, and uninvaded condition). The distance between the paired adjacent invaded and uninvaded conditions per site was approximately 50 m apart. Each invasion condition measured approximately 100 m long x 30 m wide. Within each invasion condition, five 10 × 10 m plots, each separated by a 5 m buffer were setup along a belt transect which was parallel to R578 road. The first plot started 5 m from the boundary of the selected invasion condition. The plots were marked with metal droppers. In total 45 plots (5 plots x 3 invasion conditions x 3 sites) were used for vegetation surveys.

Within each patch, the following measurements were used to determine invasion cover condition. Firstly, aerial cover estimates of *L. camara* per patch were visually assessed using Google Earth Pro Version 7.3 software [36]. Visual estimates in the uninvaded sites were based on a commonly occurring native tree species of *V. karroo*. The above-mentioned visual estimates were possible using Google Earth given that the study area is in savanna biome, which is dominated by trees and shrubs that are widely spaced so that the canopy does not close. Although Google Earth has its limitations e.g. poor spectral discrimination for cover mapping and shadowing problems, its use in this study allowed effective visual cover estimates due to its high-resolution satellite imagery. Secondly, basal stem diameter (measured 10 cm above the ground using a vernier caliper) of *L. camara* plants (in invaded conditions) and *V. karroo* (in uninvaded condition) were recorded on 20 randomly selected plants per patch. For multi-stemmed plants, only the largest stem was measured. Thirdly, plant height for all the 20 plants was measured using a ranging pole with 10 cm graduations. Results of these measurements (see Table 2) were used to categorize invasion condition as *L. camara* high and low invasion conditions and uninvaded condition. The adopted invasion conditions of high (>70%) and low (<60%) are aligned with previous studies e.g. Tererai et al. [6] who investigated the effects of *Eucalyptus camaldulensis* invasion on native vegetation along the Berg River.

Vegetation surveys

To examine species diversity in the different invasion conditions, counts of all trees and shrubs were conducted in the plot, and counts of all forbs as well as grasses were conducted in a 1 m^2 quadrat positioned at the center of the plot. Plant canopy cover percentage for trees and shrubs were estimated visually in every plot, whereas cover estimates for forbs and grasses were conducted in the above-mentioned quadrats. Canopy cover percentages of each plant species were visually estimated to the nearest 5% or 1% when species occupied <5%. Voucher specimens for all species were collected and identified at Botany Department, at the University of Venda. Species were assigned to four growth forms of trees, shrubs, forbs, and grasses based on morphology. However, due to difficulties associated with identifying and distinguishing trees and shrubs [37,38], the two growth forms were combined during data analysis. Vegetation surveys were conducted in March 2018, thus towards the end of the rainy season to optimize plant identification.

Statistical analysis

Species richness, Shannon-Wiener index, and species evenness were used to measure changes in species diversity associated with each invasion condition. Relative cover was calculated as the proportional cover of individual species as a percentage of total plant cover (based on different growth forms) per each plot. After normality and homogeneity of variance tests using Shapiro-Wilk test and Levene's test respectively, Factorial Analysis of Variance in General Linear Models (GLM) were used to test the effects of two grouping factors of invasion conditions (high, low and uninvaded) and invasion

Table 3
Species richness, Shannon-Wiener index, and evenness based on alien and native (invasion status) species abundance count from different invasion conditions. Data are mean ± se and Factorial ANOVA results are shown (***$P < 0.001$). Means with different superscript letters are significantly different.

	High invasion		Low invasion		Natural		Two-way ANOVA = F values		
	Alien	Native	Alien	Native	Alien	Native	Invasion condition	Invasion status	Invasion condition x invasion status
Species richness	5.86 ± 0.19^{d}	9.33 ± 0.21^{c}	4.40 ± 0.21^{e}	12.80 ± 0.17^{b}	0.00 ± 0.00^{f}	32.40 ± 0.75^{a}	365.13***	2995.43***	988.67***
Shannon-Wiener index	1.83 ± 0.03^{b}	0.74 ± 0.02^{e}	1.66 ± 0.02^{c}	1.05 ± 0.01^{d}	0.00 ± 0.00^{f}	3.30 ± 0.03^{a}	150.94***	874.07***	5867.87***
Evenness	0.94 ± 0.01^{ab}	0.94 ± 0.01^{ab}	0.93 ± 0.01^{b}	0.93 ± 0.01^{b}	0.00 ± 0.0^{oc}	0.95 ± 0.01^{a}	6203.50***	6836,40***	6583.90***
Species richness per growth form									
Trees and shrubs	2.47 ± 0.17^{b}	3.87 ± 0.19^{c}	2.00 ± 0.17^{b}	5.40 ± 0.19^{b}	0.00 ± 0.00^{e}	13.27 ± 0.46^{a}	121.97***	952.01***	353.16***
Forbs	1.87 ± 0.16^{cd}	2.87 ± 0.16^{bc}	1.27 ± 0.12^{d}	3.80 ± 0.26^{b}	0.00 ± 0.00^{e}	9.33 ± 0.48^{a}	53.05***	444.96***	158.63***
Grasses	1.67 ± 0.19^{cd}	2.60 ± 0.19^{bc}	1.20 ± 0.11^{d}	3.53 ± 0.19^{b}	0.00 ± 0.00^{e}	9.67 ± 0.57^{a}	61.04***	380.16***	150.01***

status (native or alien) on measured diversity indices and relative cover. The effect of relative cover of *L. camara* invasion on different invasion condition was compared using one-way ANOVA. Where ANOVAs were significantly different, Tukey's multiple comparisons tests were used to determine differences between invasion conditions and invasion status at $P < 0.05$. A regression analysis between *L. camara* canopy cover and diversity indices (total species richness and Shannon-Wiener index) was used to assess vegetation changes associated with *L. camara* invasion at plot scale. Species occupancy frequency was calculated as the number of times a species occupy different plots relative to the total number of the species in all plot. Species occupancy frequency was expressed as a percentage per invasion condition. All statistical analysis were done using Statistica version 13.1 [39].

To evaluate how invasion condition changed species composition, Principal Component Analysis (PCA) was performed using Canoco 5 [40] using presence and absence data. One-way analysis of similarity (ANOSIM), which generates a Global R statistic value, were used to test significant differences on the Bray-Curtis matrices between invasion conditions. Similarity percentage (SIMPER) analyses were used to assess the percentage contribution of each plant species to the overall similarity between invasion conditions. Both ANOSIM and SIMPER were analyzed using Primer version 6 (PRIMER-E Ltd, Plymouth, UK).

Results

Effects of L. camara *invasion on species diversity*

All indices of diversity, namely species richness, Shannon-Wiener index, and evenness differed significantly amongst the different invasion conditions and invasion status (Table 3). The Tukey's test indicated that the natural condition had higher indices (species richness, Shannon-Wiener index and evenness) than the *L. camara* high and low invasion conditions (Table 3). Invasion status comparison between the two *L. camara* invasion conditions showed that species richness and Shannon-Wiener index for alien plants were significantly higher in the *L. camara* high than low invasion conditions (Table 3). In contrast, species richness and Shannon-Wiener index for native species were significantly higher in the *L. camara* low than high invasion conditions. With regards to invasion condition there were no significant differences for evenness between the *L. camara* high and low invasion conditions (Table 3). Interactions between invasion conditions and invasion status showed significant differences for all measured indices of diversity (Table 3).

Species richness for all growth forms differed significantly amongst the different invasion conditions and invasion status (Table 3). The Tukey's test indicated that the natural condition had higher trees and shrubs, forbs, and grasses richness than the *L. camara* high and low invasion conditions (Table 3). Invasion status comparison between the two *L. camara* invasion conditions showed no significant differences between the *L. camara* high and low invasion conditions for richness of alien plants for all growth forms (Table 3). In contrast, invasion status comparison between the two *L. camara* invasion conditions for native trees and shrubs showed significantly higher richness in *L. camara* low than high invasion conditions. However, this was not the case for native forbs and grasses which showed no significant differences between *L. camara* high and low invasion conditions (Table 3). Interactions between invasion conditions and invasion status for species richness showed significant differences for all growth forms (Table 3).

Effects of L. camara *invasion on vegetation cover*

Relative cover of *L. camara* was significantly higher in the high than low invasion condition (Fig. 2a). Relative cover for all growth forms differed significantly amongst the different invasion conditions and invasion status (Fig. 2b-d). The Tukey's test indicated that the natural condition had higher relative cover for trees and shrubs and forbs than the *L. camara* high and low invasion conditions (Fig. 2b and c). For grasses, Tukey's test indicated that the *L. camara* low invasion condition had higher relative grass cover than the natural and *L. camara* high invasion conditions (Fig. 2d). Invasion status comparison between

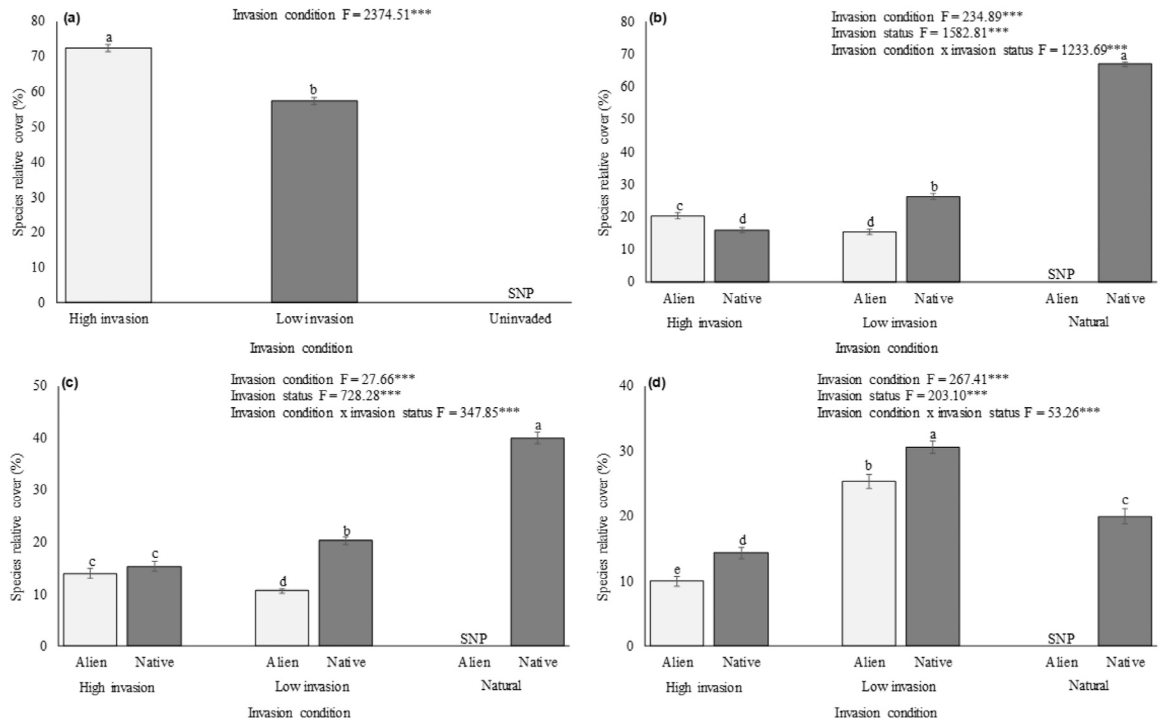

Fig. 2. Species relative cover comparisons between invasion conditions and invasion status for (a) *L. camara*, (b) trees and shrubs, (c) forbs, and (d) grasses. Bars are mean ± se and Factorial ANOVA results are shown (***$P < 0.001$). Bars with different superscript letters are significantly different. SNP means species not present.

the two *L. camara* invasion conditions for alien trees and shrubs as well as forbs showed significantly higher relative cover in *L. camara* high than low invasion conditions (Fig 2b and c). In contrast, invasion status comparison between the two *L. camara* invasion conditions for native trees and shrubs as well as forbs showed significantly higher relative cover in *L. camara* low than high invasion conditions (Fig 2b and c). Invasion status comparison between the two *L. camara* invasion conditions for both alien and native grasses showed significantly higher relative cover in *L. camara* low than high invasion conditions (Fig 2d). Interactions between invasion conditions and invasion status for relative cover showed significant differences for all growth forms (Fig 2d).

Relationship between L. camara *and species diversity*

Regression analysis revealed that species richness for both alien and native species decreased with increasing *L. camara* relative cover in both the *L. camara* high and low invasion condition, though there were no significant differences (Fig. 3a-b). Shannon-Wiener for both alien and native species increased with increasing *L. camara* relative cover in the *L. camara* high invasion condition, though there were no significant differences (Fig. 3c). There was no effect of increasing *L. camara* relative cover on Shannon-Wiener for both alien and native species in the low invasion condition, and these showed no significant differences (Fig. 3d).

Effects of L. camara *invasion on species composition*

Fifty-eight plant species were recorded across all invasion conditions, of which 29 were trees and shrubs, 15 were forbs, and 14 were grasses (Appendix 1). Across all invasion conditions, eight species (three trees and shrubs, two forbs, and three grasses) were found in all sites (Appendix 1), however, these species had high occupancy frequency in uninvaded condition as compared to *L. camara* high and low invasion condition. The eight above-mentioned species were native species of *Lippia javanica, Searsia* sp., *V. karroo, C. dactylon, Panicum maximum*, and *Aristida stipitata* as well as alien forbs of *Ipomoea* sp., and *Hermannia* sp. (Appendix 1). *Lantana camara* invasion was associated with significant change in species composition as demonstrated by the PCA ordination results (Fig. 4). PCA bi-plots of both plots and species for all growth forms showed clear species separation among the three invasion conditions (Fig. 4a-d). Most woody alien plants, e.g. *A. mearnsii, R. rigidus*, and *C. decapetala* were associated with both *L. camara* high and low invasion conditions (Fig. 4b). Most forbs and grasses assembled more in uninvaded and *L. camara* low invasion conditions as compared to *L. camara* high invasion condition (Fig. 4c-d). The first two PCA axes for all species (Fig. 4a) showed high eigenvalues and accounted for 67% of the variance.

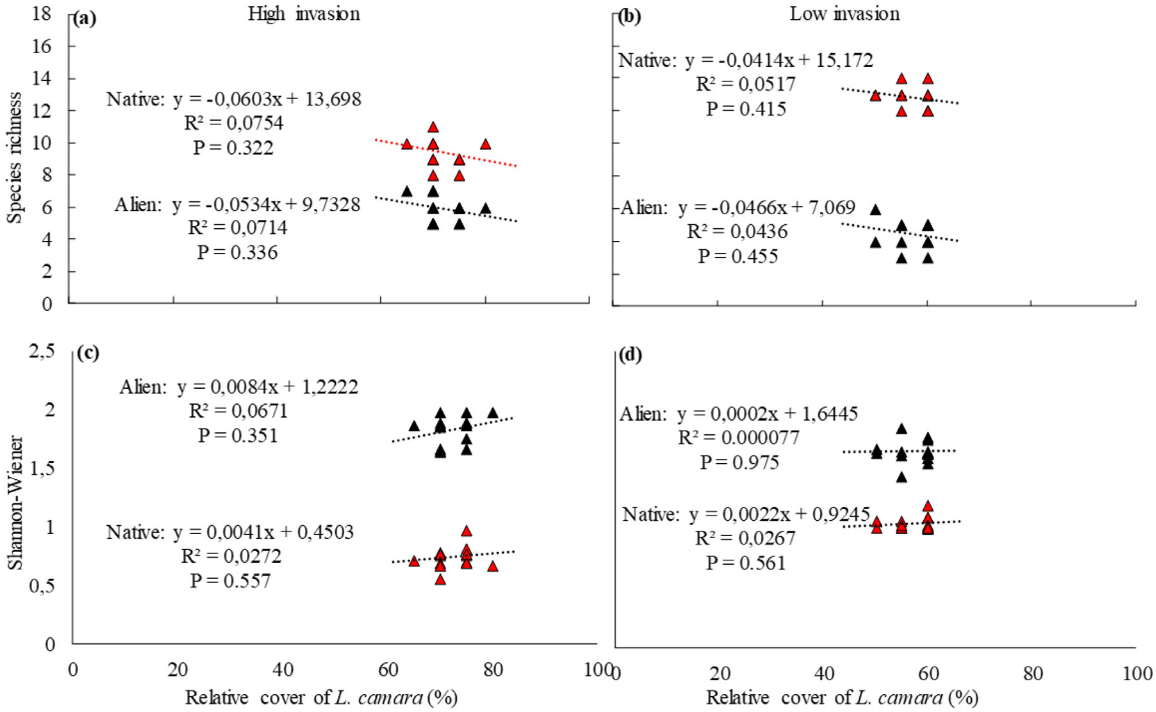

Fig. 3. Regression between *L. camara* relative cover and species richness and Shannon-Wiener for both alien and native species for (a) species richness for high invasion, (b) species richness for low invasion, (c) Shannon-Wiener index for high invasion, and (d) Shannon-Wiener index for low invasion.

Table 4
Comparison of species assemblages for different invasion conditions from different growth forms. Data shows one-way Analysis of Similarity (ANOSIM) and Similarity Percentages (SIMPER).

Growth form	ANOSIM Global R	P-value	SIMPLER (Percentage similarity) High invasion	Low invasion	Uninvaded
All plant species	0.96	0.001	68.37	75.53	89.31
Trees and shrubs	0.92	0.001	63.16	68.84	92.24
Forbs	0.81	0.001	67.75	78.71	86.72
Grasses	0.92	0.001	70.82	77.13	85.76

ANOSIM showed significant separations in community composition among the three invasion conditions for all the growth forms (Table 4). The above-mentioned community composition separations were more evident for all species combined followed by trees and shrubs, grasses and forbs (Table 4). For all species, similarity percentages (SIMPER) test showed average similarity of 68% for the *L. camara* high invasion condition, 76% for the *L. camara* low invasion condition, and 89% for the uninvaded condition (Table 4). Seven species, namely *Panicum maximum, Tragus berteronianus, Aristida adscensionis, Hermannia* sp., *Ipomoea* sp., *Searsia* sp., and *R. rigidus* contributed more than 6% to the observed similarities in *L. camara* high invasion condition. Only one species, namely *Urochloa* sp. contributed more than 6% to the observed similarities in *L. camara* low invasion condition. In the uninvaded condition, 26 species contributed more than 2% to the observed similarities. For all species, the average dissimilarity was 56% between *L. camara* high and low invasion condition, 78% between *L. camara* high invasion condition and uninvaded conditions, and 57% between *L. camara* low invasion condition and uninvaded conditions.

Discussion

This study aimed to determine changes in native plant species diversity, cover and composition associated with different *L. camara* high and low invasion conditions. Results of this study indicate that invasion by *L. camara* is associated with a decline in species diversity, cover, and composition, with such reductions being visible in both high and low L. *camara* invasion conditions. Total species richness and Shannon-Wiener index of diversity declined in both *L. camara* high and low invasion conditions, and this was noticeable for all growth forms. The above results show the pervasive threat posed by *L. camara* to native species diversity and composition. Results of this study concur with previous studies that have reported a decline in species diversity following *L. camara* invasion [25,41,42]. For example, Aravindhan and Rajendran [42] reported that *L. camara* invasion led to the decrease and degradation of native species richness, diversity, composition, and structure

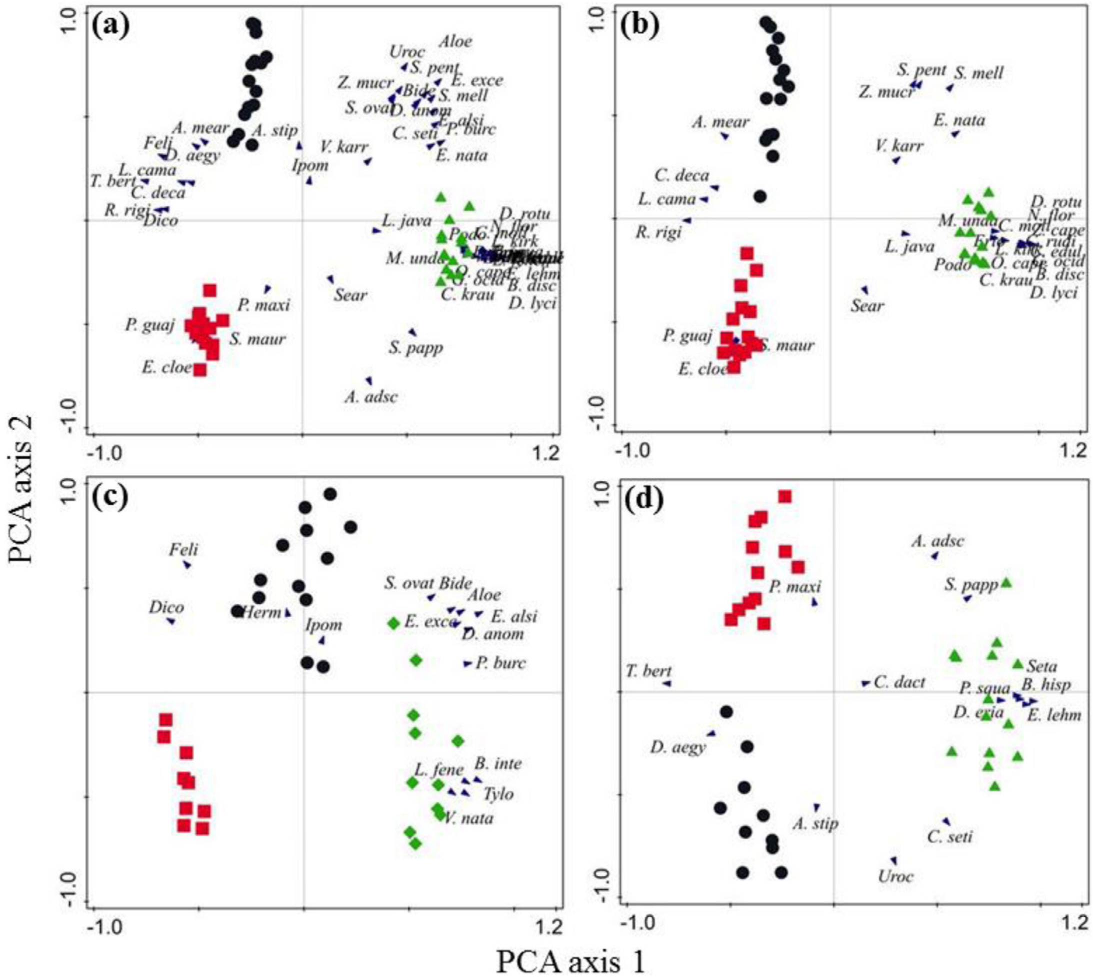

Fig. 4. Principal Component Analysis (PCA) bi-plots of species (▲) from the sites in different invasion conditions (■ = high invasion, • = low invasion, and ▲ = uninvaded) for (a) all plants, (b) trees and shrubs, (c) forbs, and (d) grasses. The first four letters of the species names are presented with full names in Appendix 1.

in the Velliangiri hills of India. Similarly, Sundaram and Hiremath [25] reported that the increase in *L. camara* abundance in Biligiri Rangaswamy Temple wildlife sanctuary in India caused a significant decline in species richness, diversity and evenness. The same above-mentioned study reported reductions in native tree population structures and tree density because of competition from *L. camara*. Turner and Downey [41] reported that some 275 native plants in Australia are under threat to *L. camara* invasion.

Several direct (e.g. competition) and indirect (e.g. habitat alterations) factors can explain the decline of species diversity and composition associated with *L. camara* invasion. Direct drivers of species decline following *L. camara* invasion can be linked to competition. Sharma et al. [43] concluded that *L. camara* outcompetes native flora for resources, e.g. nutrients, soil moisture, and sunlight. Sundaram and Hiremath [25] reported that *L. camara*, like any other invasive plant species, tend to utilize limited resources (e.g. soil nutrients) efficiently as compared to other plants thus facilitating its expansion and leading to decline of native species. This competitive interaction between *L. camara* and other species is further necessitated by the fact that *L. camara* produces allelopathic chemicals that prevent growth and establishment of other native species [44–46].

Indirect drivers that might cause species decline following *L. camara* invasion may include habitat alterations [25], and changes in the physical structure of the invaded ecosystem [46]. Sharma and Raghubanshi [25] reported that alterations in litter and soil chemistry beneath *L. camara* canopy facilitate its invasion and native species displacement. Similarly, the negative effects of *L. camara* invasion may occur due to shading which causes poor native species germination and survival of underneath light demanding seedlings of other species [47]. In this study, the effects of shading on native species should have been more visible under *L. camara* high than low invasion condition; this based on the suggestion that effects of invasion are dependent on invasion density and cover [6,48,49]. For example, Tererai et al. [6] reported a decline in native species diversity with increasing *Eucalyptus* invasion cover. Similarly, Yapi et al. [50] reported significant variations in native species basal cover between light and dense *Acacia* invasion conditions. In contrast, this study reported similar species diversity decline in both high and low invasion conditions. This could be a result of the simultaneous occurrence of direct and indirect drivers of native species change following *L. camara* invasion. The suggested simultaneous occurrence of direct and indirect drivers could also explain the observed relationship between relative cover and species diversity in the *L. camara* high and low invasion conditions.

Results of this study showed that the impact of *L. camara* invasion on species richness was observed for all growth forms (i.e. grasses, forbs, shrubs and trees), though more prevalent for trees and shrubs, an indication that shifts in vegetation structure are possible following *L. camara* invasion. Shifts in vegetation structure following *L. camara* invasion have been reported in the past. For example, Gooden et al. [5] predicted shifts in vegetation structure from tall open forest to low shrubland following *L. camara* dominance. The above-mentioned vegetation structural shifts were based on the observation that trees and shrubs are more impacted by *L. camara* invasion than herbs and grasses. However, such shifts in vegetation could vary depending on invasion density and cover. Indeed, species relative cover for trees and shrubs as well as forbs declined with increasing *L. camara* cover, this indicating a threashold impact of *L. camara* on cover of trees, shrubs and forbs. The above may represent high species resilience to *L. camara* invasion at low cover, with such resilience being lower as *L. camara* gain cover dominance [5,51]. The impact of *L. camara* invasion on native vegetation cover, particularly native trees and shrubs, can be explained by two relationships (i) the maintenance of native species at low *L. camara* invasion cover, and (ii) the loss of native species at high *L. camara* invasion cover. The first relationship might be a result to greater community stability and resilience to *L. camara* disturbance [52], whereas the second relationship might be a result of increased competition and greater resource acquisition from *L. camara* dominance [5,53].

The colonization-based saturation hypothesis, which postulates a reduction in native species displacement when an invader has reached invasion saturation point [54], can explain the presents of other woody species underneath *L. camara* invaded areas. For example woody native species of *Lippia javanica, Searsia* sp.*, and V. karroo* as well as alien plants of *E. cloeziana, A. mearnsii, Psidium guajava, R. rigidus, Solanum mauritianum,* and *C. decapetala* were present in both *L. camara* high and low invasion conditions, though more abundance was recorded in the high invasion condition (this only applicable for woody invasive alien plants). Based on the colonization-based saturation hypothesis the continuous addition of invasive alien plant density and abundance within an invaded saturated ecosystem is less likely to cause a decline of other alien co-occurring species [54]. This hypothesis is likely a result of invasion resistance [54] and invader impact thresholds [5,55]. Therefore, results of this study suggest that other alien plants that co-occur with *L. camara* can benefit from the invasion process, thus making such co-occurring species unlikely to be displaced [56]. Indeed, several studies have reported that *L. camara* can co-occur with other alien plant species [57]. Co-occurrence of plant species can be driven by the ability of different species to positively or mutually interact [58]. However, the presence of co-occurring invasive woody species underneath *L. camara* canopy has potential to negatively affect any future management interventions through the proliferation of secondary alien invaders once *L. camara* has been cleared for ecological restoration purposes. Indeed, Gooden et al. [5] confirmed that secondary invasion by other invasive alien plants occur after *L. camara* removal.

The presence of some native forbs and grasses underneath *L. camara* invaded sites seem to suggest that *L. camara* invasion does not result in total native species exclusion, thus suggesting a potential refuge effect. However, cover of such native species decreased with increasing *L. camara* invasion intensity. This result does not concur with previous studies that showed the increase in fabaceae and asteraceae species with increasing *L. camara* cover in the western Himalayan forests of India [57]. In this study, the observed presence of forbs and grasses underneath *L. camara* invaded sites could explain the reported species evenness results, which showed no differences between the two *L. camara* invasion conditions. Indeed, Tererai et al. [6] reported no significant differences in species evenness between different *Eucalyptus* invasion conditions. Previous studies have generally observed that the presence of some native forbs and grasses underneath invasive plants is a result of shade tolerant species co-occurring with the invader [6].

Conclusions

Results of this study suggest that invasion by *L. camara* at different cover conditions is a major threat to species diversity, cover, and composition in the Vhembe Biosphere Reserve, Limpopo Province of South Africa. Given that *L. camara* is a problematic invader in other parts of South Africa and the world, these results could be applicable elsewhere. The continued presence of the plant species at different cover conditions in the Vhembe Biosphere Reserve is likely to transform the natural ecosystem, therefore, management interventions to reduce invasion extent should be implemented. Such management interventions may include removal of *L. camara* and other co-occurring alien plants through alien clearing. Mechanical clearing of *L. camara* (felling the alien plants) has been shown to be effective for small stands, however, the method is costly and requires constant and meticulous follow-up [18,59]. The spraying of cut stumps using herbicides that belong to the phenoxy acid and pyridine groups has been shown to effectively prevent coppicing [18,60]. However, the effectiveness of herbicides application or chemical control of invasive alien plants in general is expensive, and depends on time of application, plant size, and mode of application [18]. Irrespective of the control method used, clearing of *L. camara* should consider protecting the existing co-occurring native species.

Declaration of Competing Interest

The author declares no conflict of interest

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Appendix 1. List of 58 frequently occurring plant species identified from different invasion conditions. (*) Indicates that the species was present and is based on calculated species occupancy frequencies categorized as * (1 – 20%), ** (21 – 40%), *** (41 – 60%), **** (61 – 80%) and **** (81 – 100) with (–) indicating that the species was not present. (N) indicates native species and (A) indicates alien plants

Species names	High invasion	Low invasion	Uninvaded
Trees and shrubs			
[A]*Eucalyptus cloeziana*	***	–	–
[A]*Acacia mearnsii*	**	****	–
[A]*Lantana camara*	*****	****	–
[A]*Psidium guajava*	***	–	–
[A]*Rubus rigidus*	****	****	–
[A]*Solanum mauritianum*	****	–	–
[A]*Caesalpinia decapetala*	***	***	–
[N]*Brachylaena discolor*	–	–	*****
[N]*Combretum kraussii*	–	–	*****
[N]*Combretum molle*	–	–	*****
[N]*Diospyros lycioides*	–	–	*****
[N]*Dombeya rotundifolia*	–	–	*****
[N]*Euclea natalensis*	–	***	*****
[N]*Grewia ocidentalis*	–	–	*****
[N]*Landolphia kirkii*	–	–	*****
[N]*Lippia javanica*	****	****	*****
[N]*Maytenus undata*	–	–	****
[N]*Nuxia floribunda*	–	–	*****
[N]*Searsia pentheri*	–	*****	****
[N]*Searsia* sp.	****	***	*****
[N]*Vachellia karroo*	****	*****	*****
[N]*Zanthoxylum capense*	–	–	*****
[N]*Ziziphus mucronata*	–	****	****
[N]*Catha edulis*	–	–	*****
[N]*Coddia rudis*	–	–	*****
[N]*Olea capensis*	–	–	*****
[N]*Eriocephalus* sp.	–	–	****
[N]*Podocarpus* sp.	–	–	****
[N]*Senegalia mellifera*	–	****	*****
Forbs			
[A]*Felicia* sp.	***	*****	–
[N]*Dicoma anomala*	–	****	*****
[N]*Tylophora* sp.	–	–	*****
[N]*Vernonia natalensis*	–	–	****
[A]*Ipomoea* sp.	****	*****	*****
[N]*Dicoma* sp.	****	****	–
[N]*Aloe* sp.	–	*****	*****
[N]*Bidens* sp.	–	****	*****
[N]*Euphorbia excelsa*	–	*****	*****
[N]*Phyllanthus burchellii*	–	***	*****
[N]*Limeum fenestratum*	–	–	*****
[A]*Hermannia* sp.	****	*****	****
[N]*Evolvulus alsinoides*	–	****	*****
[N]*Sida ovata*	–	****	****
[N]*Blepharis integrifolia*	–	–	*****

(*continued on next page*)

Species names	High invasion	Low invasion	Uninvaded
Grasses			
[N]*Coleochloa setifera*	–	****	*****
[N]*Cynodon dactylon*	****	****	*****
[N]*Setaria* sp.	–	–	*****
[N]*Digitaria eriantha*	–	–	****
[A]*Aristida adscensionis*	*****	–	*****
[N]*Eragrostis lehmanniana*	–	–	*****
[A]*Tragus berteronianus*	****	*****	–
[N]*Dactyloctenium aegyptium*	***	****	–
[N]*Pogonarthria squarrosa*	–	–	*****
[N]*Bulbostylis hispidula*	–	–	*****
[N]*Urochloa* sp.	–	*****	*****
[N]*Panicum maximum*	*****	****	****
[N]*Aristida stipitata*	***	*****	***
[N]*Schmidtia pappophoroides*	***	–	*****

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